



UNIVERSITÀ
DEGLI STUDI
FIRENZE

FLORE

Repository istituzionale dell'Università degli Studi di Firenze

Fighting behavior in hermit crabs: the combined effect of resource-holding potential and resource value in *Pagurus longicarpus*.

Questa è la Versione finale referata (Post print/Accepted manuscript) della seguente pubblicazione:

Original Citation:

Fighting behavior in hermit crabs: the combined effect of resource-holding potential and resource value in *Pagurus longicarpus* / F. GHERARDI. - In: BEHAVIORAL ECOLOGY AND SOCIOBIOLOGY. - ISSN 0340-5443. - STAMPA. - 59:(2006), pp. 500-510. [10.1007/s00265-005-0074-z]

Availability:

This version is available at: 2158/210248 since:

Published version:

DOI: 10.1007/s00265-005-0074-z

Terms of use:

Open Access

La pubblicazione è resa disponibile sotto le norme e i termini della licenza di deposito, secondo quanto stabilito dalla Policy per l'accesso aperto dell'Università degli Studi di Firenze (<https://www.sba.unifi.it/upload/policy-oa-2016-1.pdf>)

Publisher copyright claim:

(Article begins on next page)

Francesca Gherardi

Fighting behavior in hermit crabs: the combined effect of resource-holding potential and resource value in *Pagurus longicarpus*

Received: 15 February 2005 / Revised: 17 June 2005 / Accepted: 9 August 2005 / Published online: 14 October 2006
© Springer-Verlag 2006

Abstract A study was conducted to determine whether asymmetries in both resource-holding potential (RHP) and resource value (RV) influence dominance and fighting behavior in the hermit crab *Pagurus longicarpus*. A total of 120 groups of three crabs were observed for 10 min in four experiments that tested all diverse combinations of equal/different RHP (i.e. ‘body size’) and equal/different RV (i.e. ‘shell size’ and ‘shell quality’). In a fifth experiment, dominant and subordinate individuals of the same size category (26 groups) were forced to enter shells of opposite quality than those previously occupied, and then the behavior of the reconstituted original groups was observed for additional 10 min. As expected, crabs in lower quality shells were more willing to initiate and to escalate fights. However, their attacks were directed to any crab of the group, independently of the defender’s shell quality, and the fight duration did not vary with the different value of the resources at stake. This may indicate that *P. longicarpus* is unable to assess the quality of the shells available in its social environment but bases its tactical decisions during fights solely on its own resource. This suggestion was confirmed by the change in the fighting behavior of crabs whose shell quality was experimentally altered. This manipulation induced an overall increase in the intensity of aggression, drastic modification of crab behavior, and inversion of the hierarchy even though these crabs have had previous experiences of wins/losses and were familiar to the other members of the group. In this species, large

crab size and/or the occupancy of adequate (and oversized) shells appeared to be the most likely determinant of contest resolution. Individuals seemed to retain a memory of the previously held resource and behaved accordingly.

Keywords Resource value · Fighting behavior · Dominance · Hermit crabs · *Pagurus longicarpus*

Introduction

Game theory models predict that fighting between conspecifics is affected in its dynamics by asymmetries that an animal may be able to assess (e.g. Maynard Smith 1974, 1982). Apart from the effects of the different strategies that animals adopt during combats, the relative fighting ability of a contestant [i.e. resource-holding potential (RHP); Parker 1974] has been generally viewed as the main determinant of its winning or losing agonistic encounters. RHP is commonly measured from the animal’s relative body size, which most often is a reflection of the relative size of its weaponry (e.g. Caldwell and Dingle 1979; Sneddon et al. 1997). The ability of animals to assess and compare their own RHP with that of their rival, and to make decisions based on the estimated differences, has been the focus of most studies of fighting behavior, and it is integral to some theoretical models of animal conflict—i.e. the asymmetric ‘war of attrition’ (e.g. Maynard Smith and Parker 1976), and the ‘sequential’ (e.g. Enquist and Leimar 1983) or ‘cumulative assessment’ models (Payne 1998).

However, when the outcome of fights cannot be predicted from differences in RHPs or from an animals’ ability to assess them, the observed disparity between contestants has been explained on the basis of social dynamics (Chase 1982; Chase et al. 2002) or other asymmetries that may change in the course of fights (Briffa and Elwood 2004), such as the rivals’ physiological condition (e.g. Drews 1993; Sneddon et al. 1999; Briffa and Elwood 2002) and their fighting experience (‘winner

Communicated by P. Backwell

F. Gherardi (✉)
Dipartimento di Biologia Animale e Genetica,
University of Florence,
Via Romana 17,
50125 Florence, Italy
e-mail: francesca.gherardi@unifi.it
Tel.: +39-055-2288216
Fax: +39-055-222565

and loser effects'; Dugatkin 1997). Additionally, empirical evidence from a variety of taxa (reviewed in Taylor and Elwood 2003) suggests that often the dynamics of a contest depends on decision rules based solely on the RHP of the decision maker, rather than on differences in fighting ability between self and the rival (e.g. Taylor et al. 2001). The idea of an individual's 'own RHP-dependent persistence' (Taylor and Elwood 2003) has been incorporated into several theoretical models, e.g. 'war of attrition without assessment' (Mesterton-Gibbons et al. 1996) and 'energetic war of attrition' (e.g. Payne and Pagel 1996) models.

Asymmetries in the quality of the contested resource [resource value (RV)], such as mate, food, nest, or territory, play an additional role in influencing fighting intensity, its duration, and the probability of victory in a wide range of organisms—e.g. shrews (Barnard and Brown 1982), hummingbirds (Ewald 1985), several species of arthropods, amphibians, reptiles, and mammals (citations in Enquist and Leimar 1987), and sand gobies (Lindström and Pampoulie 2005). This may depend on external factors, such as detectable properties of the resource (the 'objective' resource value), and/or on internal factors (the 'subjective' resource value), i.e. the value that the combatant places on that type of resource. Therefore, when a resource yields a high fitness advantage, contest intensity may be relatively high—e.g. in hummingbirds (Dearborn 1998) and honey bees (Gilley 2001), but not in the fallow deer (Jennings et al. 2004)—compared with low-quality resources (e.g. in the speckled wood butterfly; Davies 1978). A previous investment in the held resource may increase its value for the owner (e.g. the nest in the European robin; Tobias 1997), who will be more willing to take risks and to expend time and energy for its defense (e.g. in sand gobies; Lindström and Pampoulie 2005). A disparity between contestants may also derive from the owner being better informed of the value of the resource it possesses than the intruder—e.g. female iguanas competing for nesting burrows (Rand and Rand 1976) or male spiders competing for females (Austad 1983).

Finally, as soon as a dominance hierarchy has been formed, the relatively stable polarity in the outcome of fights may result from a form of recognition between contestants that have had experience at interacting together (Ydenberg et al. 1988). Repeated exposure to an opponent most often reduces fight intensity, e.g. in American lobsters (Karavanich and Atema 1998) and lizards (López and Martín 2001), and usually leads to high-ranking individuals monopolizing a disproportionate share of the available resources (Wittenberger 1981).

Hermit crabs offer an ideal opportunity to study correlates of fighting behavior. The strong association between the majority of hermit crab species (for exceptions see Gherardi 1996a) and empty gastropod shells greatly influences this and almost all aspects of the biology of the species in this taxon (Hazlett 1981). Having a shell of appropriate size and type provides advantages to its inhabitant, the crab being protected from mechanical

abuse, dehydration, temperature extremes (Reese 1969; Taylor 1981), salinity changes (Davenport et al. 1980), and predatory pressure (Vance 1972a). A shell that is too small will inhibit growth (Markham 1968; Fotheringham 1976a, b; Bertness 1981a; Angel 2000), reduce protection against predators (Vance 1972a; Angel 2000), and lower survival (Bertness 1981b; Borjesson and Szelistowski 1989) and reproductive success in both males (Hazlett 1989) and females (Childress 1972; Fotheringham 1976b; Bertness 1981a; Wilber 1989; Elwood et al. 1995). On the other hand, a shell that is too large makes locomotion energetically wasteful (e.g. in terrestrial hermit crabs; Herreid and Full 1986) and has negative effects on female reproduction (Fotheringham 1980). As a consequence, there is a strong selective pressure for crabs to obtain a shell of appropriate size.

Empty shells (hermit crabs are unable to directly prey on living snails; see, Rutheford 1977, for an exception) are usually in acutely short supply in the habitat (Provenzano 1960; Vance 1972b; Fotheringham 1976c; Kellogg 1976; Scully 1979; for exceptions, see Wilber and Herrnkind 1984; Gherardi et al. 1994). They may be found following snail death at gastropod predation sites (Rittschof 1980a,b; Katz and Rittschof 1993; Rittschof et al. 1995; Gherardi and Atema 2005a), but shells are most often obtained by negotiation (Hazlett 1978, 1980) or interference competition (Hazlett 1966a) with con- and heterospecifics. Several laboratory studies have shown that the decision made by a crab—whether to fight, to escalate an encounter, or to retreat—is based on its ability to assess both shell quality (Elwood and Neil 1992; Hazlett 1996; Wada et al. 1997) and the fighting ability of its opponent (Briffa and Elwood 2000a,b).

Notwithstanding the extensive literature on this topic, there have been few systematic studies (see Elwood et al. 1998; Briffa and Elwood 2001) on the multiple effects of RV, RHP, and other non-strategic variables on hermit crabs' fighting behavior. In the present study, I investigated whether asymmetries in shell quality and body size, together with previous fighting experience and familiarity with the opponents, influenced the agonistic behavior of the hermit crab *Pagurus longicarpus*.

I analyzed the groupings of three crabs arranged into four sets according to the four possible combinations of equal/different body size and equal/different shell quality. It was predicted that crabs occupying low-quality shells should be more willing to take risks fighting crabs in better-quality shells (Hazlett 1970a; Elwood 1995; Gherardi 1996b; Elwood et al. 1998). Larger crabs should be advantaged (Hazlett 1966b, 1970a), but animals having more to gain and therefore being more strongly motivated to escalate fights should be more likely to win. Finally, by experimentally altering the shell quality of crabs that were familiar with each other, it was expected that experience of previous wins/losses and recognition of opponents (Gherardi and Tiedemann 2004a) would play a role in determining the outcome of contests.

Materials and methods

Subjects, collection, and housing conditions

The long-clawed hermit crab, *P. longicarpus* Say 1817, is common in shallow waters along the western Atlantic coasts of North America, from Nova Scotia south to eastern Florida, and in the northern Gulf of Mexico from the west coast of Florida to Texas (Williams 1984).

Between July and August 2003, about 400 hermit crabs with a major chela width (CW) of 0.1–0.4 mm (corresponding to individuals with a shield length of about 4–6 mm) were randomly hand-collected from Little Sippewissett salt marsh (Massachusetts, USA) during diurnal low tides. Immediately after capture, the crabs were separated into small groups and transferred to the Marine Biological Laboratory in Woods Hole, where they were maintained in groups of up to 25 individuals in a temperature-controlled room (22°C) and under a natural 14 L:10 D cycle. They were kept in separate 20-l holding aquaria containing constantly aerated seawater, and fed a diet of commercial shrimp pellets every third day. Water was changed weekly. After being used in the experiments, crabs were released at the collection site.

General methods

Experiments were staged in opaque plastic bowls (10 cm diameter), containing 160 ml unfiltered seawater at 22°C, illuminated during observations by a 75-W incandescent light, 50 cm above the water level. Observations were always conducted between 0900 and 1700 hours.

Two days before the experiments commenced, three intact crabs were selected for each experimental group ('trio'). The animals of each trio were taken from separate holding aquaria to ensure they had no prior knowledge of one another. Sex was not noted, since sex has been shown to exert no effect on agonistic interactions in this and other hermit crab species (Winston and Jacobson 1978; Hazlett 1966b), at least during the non-reproductive period (this species reproduces between October and May with a peak in the autumn; Wilber 1989).

To obtain individuals occupying shells of the proper size for every experiment (see below), crabs were extracted from their original shell by gently breaking it with a bench vise. Each of them was then allowed 4 h alone to choose a new shell from five empty, undamaged, similarly sized shells. These shells were prepared by collecting live periwinkle *Littorina littorea* (the dominant shell type

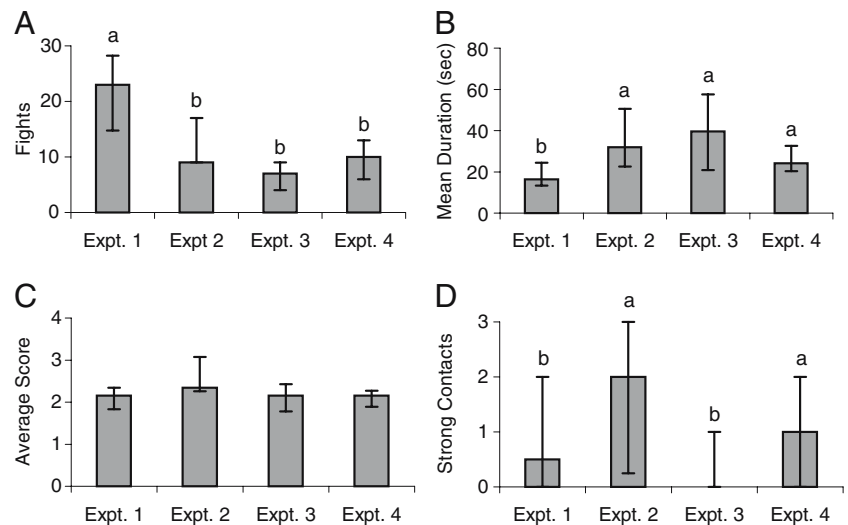
Table 1 Experimental design

	Animal #1	Animal #2	Animal #3
Expt. 1 ($n=30$)			
Crab size (\diamond)	L (0.35)	M (0.26)	S (0.15)
Shell size (\diamond)	L (19.7)	M (17.2)	S (12.6)
Shell quality (=)	OPT	OPT	OPT
Expt. 2 ($n=30$)			
Crab size (=)	M (0.32)	M (0.31)	M (0.31)
Shell size (\diamond)	L (19.4)	M (17)	S (14.4)
Shell quality (\diamond)	LTO	OPT	STO
Expt. 3 ($n=30$)			
Crab size (=)	M (0.31)	M (0.31)	M (0.31)
Shell size (=)	M (17.4)	M (17.4)	M (17.4)
Shell quality (=)	OPT	OPT	OPT
Expt. 4 ($n=30$)			
Crab size (\diamond)	L (0.37)	M (0.3)	S (0.21)
Shell size (=)	M (17.2)	M (17.2)	M (17.4)
Shell quality (\diamond)	STO	OPT	LTO
Expt. 5 ($n=26$)			
Crab size (=)	M (0.32)	M (0.31)	M (0.31)
Shell size (\diamond)	S (13.54)	M (16.87)	L (19.46)
Shell quality (\diamond)	STO	OPT	LTO

The symbols \diamond and = denote where the crabs of each group differed or were equal in terms of 'crab size', 'shell size', and 'shell quality'. Expt. 5 was a continuation of Expt. 2, using the same individuals. After Expt. 2, animals #1 and #3 were subject to an experimental shell change, leading to the alteration of their quality. So, in Expt. 5 animal #1 occupied STO shells and animal #3 LTO shells

Categories of crab and shell sizes (mean size, in mm, in parentheses): *L* large, *M* medium, *S* small. *OPT* Optimal shells, *LTO* shells that were 10% larger than the optimal shells for a given crab size, *STO* shells that were 10% smaller than the optimal shells for a given crab size, *n* sample size

Fig. 1 Number (a) and mean duration (b) of fights, average score (c), and frequency of strong contacts (d) (medians and interquartile ranges) compared among four experiments. Sample size was 30 per experiment. Letters over bars indicate the hierarchy obtained by applying multiple comparisons tests to the experiments showing a significant difference after Kruskal–Wallis one-way analyses of variance



used by the study population), boiling and removing the flesh, rinsing the shells several times in seawater, and air-drying them. Crabs were kept isolated for a total of 2 days, a period that was necessary to reset their social experience. Ten minutes before constituting the trios, the length of antennae and the color of cheliped and pereopod of the three crabs were recorded, and their shells were marked by zero, one, or two dots of permanent black ink to permit identification by the observer.

Experimental design

The influence of ‘crab size’, ‘shell size’, and ‘shell adequacy’ on the fighting behavior of *P. longicarpus* were studied, following in part the design of Gherardi et al. (in press). Crab size (an index of RHP) was estimated from the major chela width (CW, in mm) and was categorized as

large, L (CW>0.33 mm), medium, M (CW=0.23–0.33 mm), or small, S (CW<0.23 mm).

Shells were classified based on size [estimated from their length in mm; shell length (SL)] and their adequacy for the body size of the inhabiting crabs. In fact, although hermit crabs can have preferences for various characteristics of shells (size, species, and amount of damage; see, e.g. Vance 1972a; Bertness 1980, 1981c; Wilber 1990), particularly in the case of the study species (Wilber 1990), size is the most important determinant for shell selection.

Shells were categorized as L (SL>18 mm), M (SL=15–18 mm), and S (SL<15 mm). Shells that were adequate (i.e. optimal, OPT) for crabs of a given size were computed by regressing the equation $y=37.9x+7.3$, where y is SL and x is CW (both in mm). This equation was obtained from a preliminary free-choice experiment in which 192 crabs were separately allowed to choose among five empty shells of different sizes. Shells with a length 10% greater, or 10% smaller, than the OPT for a particular crab were defined

Fig. 2 Frequencies (in percentage) of individuals’ (classified per rank) fighting (a), attacking a rival (b), being attacked by a rival (c), and winning (d) (medians and interquartile ranges) compared among four experiments. Sample size was 30 per experiment (and per rank). See Fig. 1 for the meaning of letters over bars

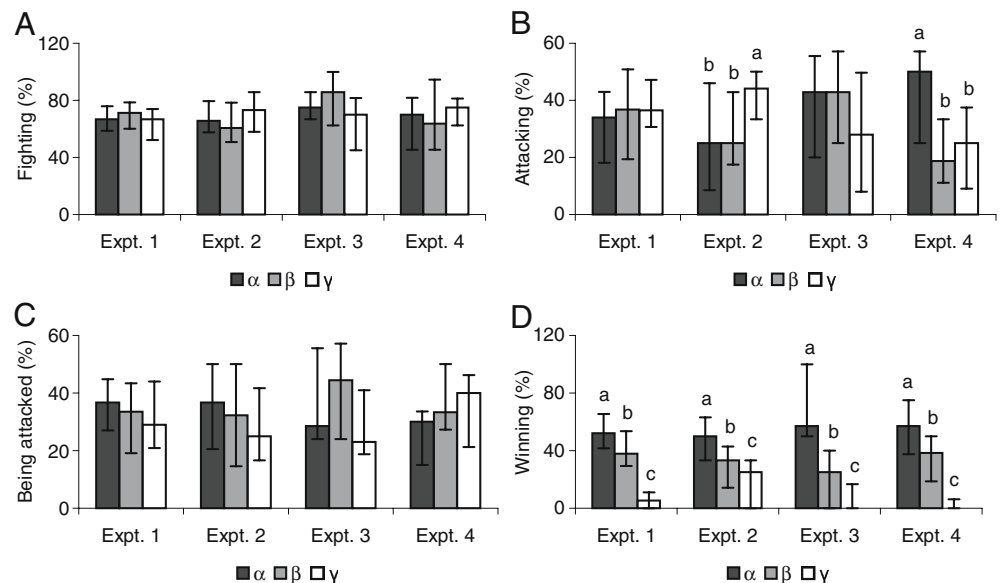


Table 2 Comparisons among ranks (α , β , and γ) in each experiment (Expts. 1–4) for the relative frequencies of individuals' fighting, attacking a rival, being attacked by a rival, and winning

	Expt. 1			Expt. 2			Expt. 3			Expt. 4		
	Fr	<i>P</i>	Hierarchy	Fr	<i>P</i>	Hierarchy	Fr	<i>P</i>	Hierarchy	Fr	<i>P</i>	Hierarchy
Fighting	4.114	0.1278	$\alpha=\beta=\gamma$	4.331	0.1147	$\alpha=\beta=\gamma$	0.738	0.6913	$\alpha=\beta=\gamma$	0.092	0.9549	$\alpha=\beta=\gamma$
Attacking	3.25	0.1969	$\alpha=\beta=\gamma$	10.294	0.0058	$\gamma>\alpha=\beta$	1.9	0.3867	$\alpha=\beta=\gamma$	5.645	0.0595	$\alpha>\beta=\gamma$
Being attacked	2.467	0.2913	$\alpha=\beta=\gamma$	3.298	0.1932	$\alpha=\beta=\gamma$	3.524	0.1717	$\alpha=\beta=\gamma$	0.738	0.6913	$\alpha=\beta=\gamma$
Winning	83.18	0	$\alpha>\beta>\gamma$	10.683	0.0048	$\alpha>\beta>\gamma$	24.441	0	$\alpha>\beta>\gamma$	19.509	0.0001	$\alpha>\beta>\gamma$

Analysis was performed using Friedman two-way ANOVA (Fr statistic, $df=2$). In the case of significance, a multiple comparisons test was applied to determine the hierarchy. Significant results are shown in bold

as 'larger-than-optimal' (LTO), or 'smaller-than-optimal' (STO) shells. Ranges of crab and shell size used were chosen so that L, M, and S shells were OPT for L, M, and S crabs, respectively.

Four experiments, structured on the basis of crab size, shell size, and shell adequacy, were run on a total of 120 trios (30 per experiment) (Table 1). In Expt. 1, each trio was composed of crabs of three size categories (L, M, and S), each occupying an OPT shell for its size (i.e. L, M, and S crabs inhabiting L, M, and S shells, respectively). Crabs of the trios used in Expt. 2 were of the same M size but differed in terms of the size of their shell (L, M, and S) and hence for their shell adequacy (i.e. LTO, OPT, and STO for crabs in L, M, and S shells, respectively). In Expt. 3, crabs in each trio had the same M size and inhabited the same OPT shell, which was of the M size category. In Expt. 4, trios were composed of L, M, and S crabs inhabiting shells of the same M size and hence of different relative adequacy (i.e. STO, OPT, and LTO shells for L, M, and S crabs, respectively).

Experiment 5 was a continuation of Expt. 2. After 1 day of cohabitation, the shell quality of crabs occupying L and S shells was switched by gently breaking their shells with a bench vise and forcing them to enter a novel shell. This shell was S, and hence STO, for the former crabs in L shells and L, and hence LTO, for the former crabs in S shells. After 4 h apart (not long enough to forget former opponents; Gherardi and Atema 2005a), 26 trios were reconstituted (in the remaining four groups one crab was

injured during the manipulation) with the same individuals as in Expt. 2 and observed their behavior for 10 min.

Data collection

Three crabs were placed in the experimental bowl and the events occurring during a 10-min observation period were recorded on a voice tape. Records were later analyzed to obtain the following details:

1. The overall number of fights and the percentage of fights undertaken by each individual. Fights were defined as interactions that started when one crab approached one or two rivals and ended when one or two opponents retreated to a distance greater than 3 cm for at least 10 seconds.
2. The duration of fights (in seconds).
3. The average score. Following in part Gherardi and Tiedemann (2004a), fights were classified as: avoidance (i.e. one opponent retreated with no overt response by the other); threat (i.e. one opponent retreated when the other extended its chelipeds or raised its pereopods or flicked its antennae or chelipeds—when partly withdrawn into the shell); contact (i.e. one opponent retreated after the occurrence of at least one contact behavior, such as antennal contact, grasp, or strike); and shell fight (i.e. one opponent retreated after the other had executed at least one bout of shell rapping).

Table 3 Comparisons among ranks (old/new α , β , and old/new γ) in Expts. 2 and 5 for the relative frequencies of individuals' fighting, attacking a rival, being attacked by a rival, and winning (26 trios)

	Expt. 2			Expt. 5		
	Fr	<i>P</i>	Hierarchy old α and γ	Fr	<i>P</i>	Hierarchy new α and γ
Fighting	6.607	0.0368	$\gamma>\alpha=\beta$	3.322	0.1899	$\alpha=\beta=\gamma$
Attacking	0.905	0.6361	$\alpha=\beta=\gamma$	1.857	0.3951	$\alpha=\beta=\gamma$
Being attacked	1.374	0.5031	$\alpha=\beta=\gamma$	2.574	0.2761	$\alpha=\beta=\gamma$
Winning	10.336	0.0057	$\alpha>\beta>\gamma$	30.471	0	$\alpha>\beta>\gamma$

Old α (and old γ) were the individuals that were dominant (and subordinate) in Expt. 2 but became subordinate (and dominant), i.e. new γ (and new α), in Expt. 5 after having been subjected to an experimental shell change (see Table 1). Analysis was done using

the Friedman two-way ANOVA (Fr statistic, $df=2$). In the case of significance, a multiple comparisons test was applied to determine the hierarchy. Significant results are shown in bold

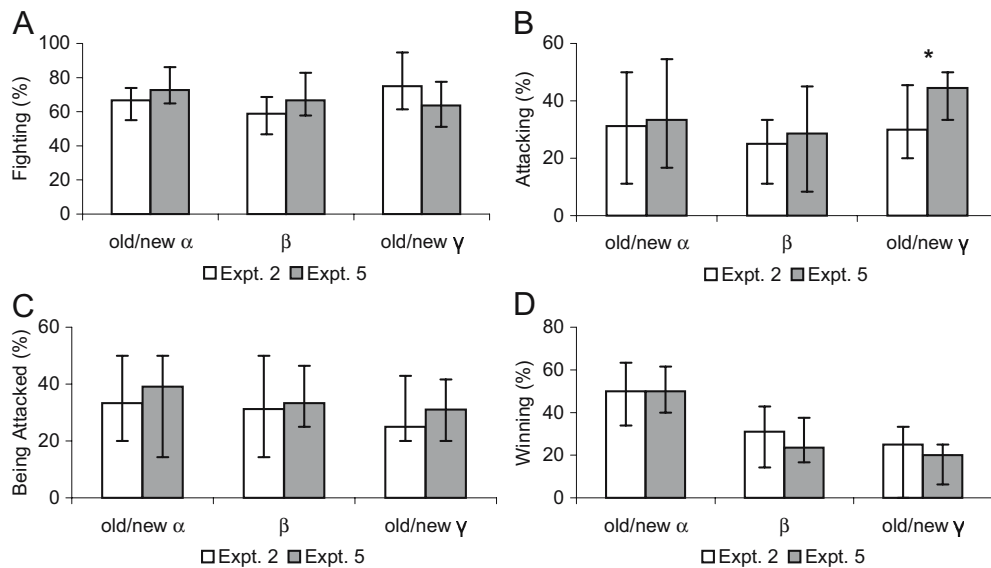


Fig. 3 Frequencies (in percentage) of individuals (classified per rank) fighting (a), attacking a rival (b), being attacked by a rival (c), and winning (d) (medians and interquartile ranges), compared between the 10-min observations that preceded (Expt. 2) and followed (Expt. 5) the experimental intervention on α and γ individuals of Expt. 2. This consisted in forcing α individuals of Expt. 2 [old α , originally in larger-than-optimal (LTO) shells] and γ

individuals of Expt. 2 [old γ , originally in smaller-than-optimal (STO) shells] to occupy STO and LTO shells, respectively. After the experimental shell change, hierarchy was inverted so that the new α (and the new γ) are the old γ (and the old α) individuals. Sample size was 26 per experiment (and per rank). * means $P < 0.05$ after Wilcoxon signed-rank tests

and, eventually, had evicted it from the shell). Each type of fight was ranked on a scale of intensity from 1 to 4. For every 10-min observation, the sum of the scores for each fight was calculated and divided by the number of fights to obtain the average score.

4. The number of grasps and strikes delivered, classified as strong contacts.
5. The occurrence of shell exploration (for a description of shell exploration in *P. longicarpus*, see Scully 1986).
6. Instances of each individual's attacking, and being attacked by, an opponent.
7. The wins recorded by each individual. The winner was the contender that did not retreat at the end of the interaction or that retreated after the other(s) withdrew into the shell.
8. Dominance, measured from the number of wins that each crab gained. From this value, the α (dominant), β , and γ (subordinate) individuals were identified. Dominance reversals were never observed during any 10-min observation.

Data analysis

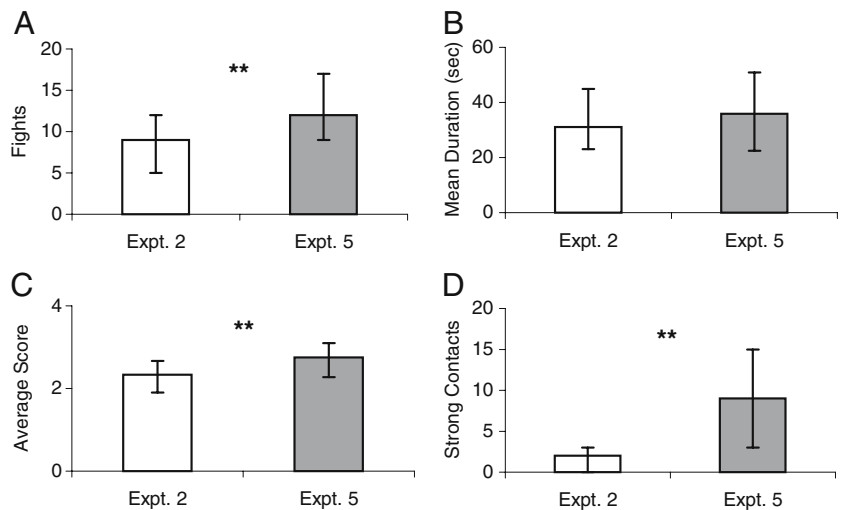
Nonparametric tests (Sokal and Rohlf 1969; Siegel and Castellan 1988) were applied, because the assumptions of normality and homogeneity of variance were not always met and some measures represented ordinal data. To examine the differences between experiments, Kolmogorov–Smirnov two-sample tests (statistic: KS) and Kruskal–Wallis one-way analyses of variance (statistic: KW) were used. Differences within trios and between Expts. 2 and 5 were analyzed by Wilcoxon signed-rank tests (statistic: z) and Friedman two-way analyses of variance (statistic: Fr) for related samples. When the null hypothesis was rejected after Kruskal–Wallis one-way analyses of variance and Friedman two-way analyses of variance, a multiple comparisons test (Siegel and Castellan 1988) was used to determine which pairs of samples differed significantly. Frequency data were analyzed with G tests. Text and figures provide medians and interquartile ranges (first–third quartiles). P values of less than 0.05 were considered statistically significant.

Table 4 Comparisons between Expts. 2 and 5 for each rank (old/new α , β , and old/new γ , see Table 3) for the relative frequencies of individuals' fighting, attacking a rival, being attacked by a rival, and winning

	Old/new α		Old/new β		Old/new γ	
	z	P	z	P	z	P
Fighting	−0.876	0.3813	−1.117	0.2638	1.653	0.0983
Attacking	−1.108	0.2678	0.384	0.7008	1.894	0.0582
Being attacked	0.84	0.4009	−0.706	0.4802	−0.161	0.8722
Winning	−1.461	0.1439	0.401	0.6883	0.865	0.3869

Analysis was done using the Wilcoxon signed-rank test (z statistic). Significant results are shown in bold

Fig. 4 Number (a) and mean duration (b) of fights, average score (c), and frequency of strong contacts (d) (medians and interquartile ranges) compared between the 10-min observations that preceded (Expt. 2) and followed the experimental intervention on α and γ individuals (Expt. 5); (see Fig. 3). Sample size was 26 per experiment. ** means $P < 0.01$ after Wilcoxon signed-rank tests



Results

Effect of RV and RHP

Dominant individuals were most often the crabs with L body size that occupied OPT (in Expt. 1, 27 vs. 3) or even STO (in Expt. 4, 30 vs. 0) shells. The influence of crab size on the probability of victory was clear also in Expt. 3. Small differences in shell size (0.1–1 mm) did not seem to influence dominance (α was the crab with a larger shell in 19 of 30 trios, $G=2.124$, $df=1$, $P>0.1$), whereas differences in body size of only 0.01–0.05 mm were sufficient to determine the dominance of the larger crab (21 vs. 9, $G=4.856$, $df=1$, $P<0.05$). In contrast, when the difference in shell size was large (Expt. 2), the individuals occupying larger, but LTO, shells most often won over similarly sized rivals (30 vs. 0).

Fights were significantly more numerous (KW=61.094, $df=3$, $P=0$; multiple comparisons test: Expt. 1>Expt. 2=Expt. 3=Expt. 4) but shorter (KW=31.753, $df=3$, $P=0$; multiple comparisons test: Expt. 2=Expt. 3=Expt. 4>Expt. 1) in Expt. 1 than in all the other experiments (Fig. 1a,b). The four experiments did not differ in the average score for fights (KW=6.158, $df=3$, $P=0.1042$) (Fig. 1c). However, strong contacts were more often executed in Expts. 2 and 4 (KW=12.867, $df=3$, $P=0.0049$; multiple comparisons test: Expt. 2=Expt. 4>Expt. 1=Expt. 3) (Fig. 1d).

Fight duration was expected to be longer when a contestant occupied a low-quality shell, other factors (i.e. hierarchical rank and social environment) being equal. Thus, the fights undertaken by similarly sized α or γ individuals were analyzed and their average duration between instances in which α or γ occupied OPT shells (in Expts. 1 and 3 for α and γ , respectively) and instances in which α or γ occupied STO shells (in Expts. 4 and 2 for α and γ , respectively) were compared. Both α and γ individuals in STO shells fought for a significantly longer time than individuals of the same rank and size in OPT shells (α : KS=0.283, $P=0.0158$; γ : KS=0.267, $P=0.0276$). However, a crab's decision to continue a contest seemed to be

relatively independent of the value of the opponent's shell. In fact, in no experiment was there a significant difference in fight duration among the three pairs ($\alpha\beta$, $\beta\gamma$, and $\alpha\gamma$) (Expt. 1: Fr=2.867, $df=2$, $P=0.2385$; Expt. 2: Fr=2.636, $df=2$, $P=0.2673$; Expt. 3: Fr=4.353, $df=2$, $P=0.1134$; Expt. 4: Fr=0.867, $df=2$, $P=0.6483$).

Individuals of different ranks were involved in the same relative number of fights in every experiment (Fig. 2a; Table 2). Only in Expts. 2 and 4, as expected, were attacks most often performed by γ and α , respectively, both occupying STO shells (Fig. 2b; Table 2). However, in none of the experiments were attacks directed at a preferential crab (Fig. 2c; Table 2). Specifically, β and γ individuals did not appear to attack the rival that had a larger or a better quality shell (β in Expt. 1: $z=-1.109$, $P=0.2673$; β in Expt. 2: $z=1.068$, $P=0.2857$; γ in Expt. 2: $z=0.322$, $P=0.7471$).

By definition, α won the majority of fights in all the experiments, followed in the hierarchy by β and γ (Fig. 2d; Table 2). Shell exploration was a rare event, being recorded in 13 instances only (from a total of the 120 trios analyzed).

Effect of win/loss experiences and familiarity with the opponents

In Expt. 2 the individuals occupying LTO and STO shells were α and γ , respectively. After the experimental shell change, the former (old) α (now in STO shells) and the former (old) γ (now in LTO shells) behaved as subordinate (new γ) and dominant (new α) individuals, respectively. In both experiments, crabs of diverse ranks did not appreciably differ for the analyzed parameters, except for the number of fights in Expt. 2 and, obviously, for the number of wins (Table 3). The new α and γ behaved as the old α and γ , as shown from the relative frequencies of the fights (Fig. 3a; Table 4), of the attacks made and suffered (Fig. 3b, c; Table 4), and of the wins gained (Fig. 3d; Table 4). The new γ , which had experienced a higher-quality shell on the previous day, made significantly more attacks than the old γ . However, also in Expt. 5, β 's and γ 's attacks were

directed to any rival without discrimination (β : $z=1.727$, $P=0.0842$; γ : $z=-1.411$, $P=0.1581$).

The number of fights ($z=-3.246$, $P=0.0012$; Fig. 4a), the average score ($z=-2.707$, $P=0.0068$; Fig. 4c), and the frequency of strong contacts executed ($z=-4.577$, $P=0$; Fig. 4d), but not the mean duration of fights ($z=0.027$, $P=0.9786$; Fig. 4b), were significantly higher after the experimental shell change. This did not seem to be a result of the disturbance inflicted on the crabs through manipulation, because aggression increased in all the individuals, β included (fights: old/new α , $z=-2.926$, $P=0.0034$; β , $z=-3.252$, $P=0.0011$; old/new γ , $z=-2.926$, $P=0.0034$; approaches: old/new α , $z=-2.515$, $P=0.0119$; β , $z=-2.49$, $P=0.0128$; old/new γ , $z=-0.396$, $P=0.692$; strong contacts: old/new α , $z=-3.868$, $P=0.0001$; β , $z=-3.31$, $P=0.0009$; old/new γ , $z=-2.161$, $P=0.0307$).

As in the other experiments, in Expt. 5 shell exploration was a rare event (three out of 26 trios).

Discussion

This study partly corroborates earlier findings showing that, in a large number of animal species, competition for resources is the main trigger for fights between conspecifics (reviewed by Huntingford and Turner 1987). In accordance with Enquist and Leimar (1987), resource value emerged here as an important non-strategic variable in fighting behavior. In fact, shell quality significantly affected the intensity of aggression, as revealed by the frequent strong contacts that crabs executed when occupying shells that were too small (i.e. in Expts. 2 and 4). Also, the individuals inhabiting shells whose size was smaller than optimal ones (γ in Expt. 2 and α in Expt. 4) were highly motivated to initiate fights and to persist with those fights.

These results are not surprising. The suitability of the occupied shells for species, size/volume, and status has been shown to exert a strong effect on intra- and inter-specific fighting behavior in the majority of studies conducted so far (Hazlett 1970a,b; Vance 1973; Grant and Ulmer 1974; Hazlett 1978, 1980; Gherardi 1996b). The increased motivation to fight in hermit crabs occupying shells too small by size/volume is also understandable as a behavioral strategy to accommodate individual growth, to protect themselves from predators, and to increase their reproductive success (see references above). However, small crabs, even if highly motivated, did not have a high probability of victory.

In contrast, crabs occupying shells that were too large (in Expts. 2 and 5) only rarely initiated fights and were more likely to be the winners. The potential disadvantages of wearing shells that were too large, e.g. the energetic costs of locomotion (Herreid and Full 1986), may therefore conceal adaptive functions. For instance, by accepting or even selecting an oversized shell crabs may, on one hand, delay the need to find larger shells to assure their growth and reproduction (Childress 1972; Wada et al. 1997; Côté

et al. 1998) and, on the other, gain some fighting advantages. This confirms previous findings in other hermit crab species (Hazlett 1970b), but requires further studies in order to understand if this competitive superiority might be attributable to the shell appearing larger to the opponents or feeling larger to the inhabiting crabs.

When the objective resource value and other factors are equal (see references in Vye et al. 1997; Gherardi and Cioni 2004), body size is important in predicting the outcome of contests even when the larger crab occupies an inadequate shell (Expt. 4) (Hazlett 1966a,b; Elwood and Glass 1981; Dowds and Elwood 1985) and is more important than shell size when differences between contestants are small for these two attributes (Expt. 3). Indeed, a similar large-body size advantage in dominance is widely diffused across the animal kingdom (reviews in, e.g., Caldwell and Dingle 1979; Archer 1988), but proximate causes of this advantage have been largely unexplored.

P. longicarpus inhabiting optimal shells (Expts. 1 and 3) made less frequent use of strong behavioral patterns even if larger shells were available in its social environment (Expt. 1). This proved true, notwithstanding that encounters were relatively more numerous (at least in Expt. 1), probably due to the higher activity of crabs wearing shells of an adequate size for their body. A possible explanation is that in this species motivation to fight changes in response to the subjective—rather than to the objective—resource value. In other words, *P. longicarpus* seems to be more willing to initiate fights and to persist with these fights when it perceives the inadequacy of its own shell rather than when it sees (or it smells, Gherardi and Tiedemann 2004b) other crabs occupying a shell of an absolute higher quality.

Indeed, my results raise doubts about the capacity of this species to finely compare the quality of the domicile shell with the quality of the shells held by the opponents. In fact, I found that hermit crabs were not choosy in their attacks but approached any individual of the group, independently of the defender's resource value. Neither did the crabs seem to gather much information about the contested resource as the fight progresses. In fact, fight duration was independent of the different quality of the shells at stake. Also, shell exploration, consisting here of a quick inspection of the outer surface of shells, was a rare event and rapping (which may be used to assess the defender's shell quality, Hazlett 1980; for other functions, see Elwood and Neil 1992; Briffa and Elwood 2000a,b) was even rarer. These results are in accordance with previous laboratory studies revealing that *P. longicarpus* is inaccurate in distinguishing shells by sight (Gherardi and Tiedemann 2004a), most often switching shells without prior investigation (Scully 1986). A confirmation comes from field observations (Tricarico and Gherardi, personal communication), showing that, upon arriving at a gastropod predation site, *P. longicarpus* quickly enters a novel shell but does not abandon its domicile shell until it has tried the new one. Possibly, the decision to keep the novel shell or to return to the old one requires some proprioceptive information that the crab is able to acquire only by wearing it.

In the overwhelming majority of the species studied so far, fighting crabs were shown, first, to make fine distinctions between a shell available in the habitat and the current domicile shell (e.g. Hazlett 1981; Jackson and Elwood 1989) and, second, to predict their fitness gains from the possession of the opponent's shell. Within the frame of game theory and of other theoretical models (e.g. Parker and Rubenstein 1981; Enquist and Leimar 1983), several authors suggested that the ability to detect and to compare fighting ability and resource value between self and the rival allows hermit crabs to make adaptive decisions, relative to the duration of shell investigation (Neil and Elwood 1986), whether or not to escalate shell fights (Hazlett 1987), and whether to flee or to persist in these fights (Hazlett 1980). A long list of studies confirms the importance of such 'mutual assessment' in the fighting dynamics of several other organisms—e.g. red deer (Clutton-Brock et al. 1979), scorpionflies (Thornhill 1984), and frogs (Burmeister et al. 2002). Conversely, a number of alternative theoretical models describe asymmetric contests in which rivals select persistence based solely on their own RHP (e.g. Mesterton-Gibbons et al. 1996; Payne and Pagel 1996). This idea led to a re-examination of the existing literature and to the identification of several anomalies concerning the mutual assessment theory (Taylor and Elwood 2003). Fighting in *P. longicarpus* might be an additional example of behavior based on decision rules of the type 'own RV-dependent persistency' (in which RV replaces RHP in Taylor and Elwood's 2003 definition).

Experience of dominance and familiarity with similarly sized opponents appear to confer little advantage to individual crabs when the quality of their shells has been experimentally degraded (Expt. 5). This contrasts with results gained from other model organisms (e.g. the crayfish *Procambarus clarkii*), in which recent wins or losses were found to alter the likelihood of an individual winning encounters even when there was a size disparity (Daws et al. 2002). Neither did status recognition (see, e.g. Zulandt et al. 1999; Gherardi and Daniels 2003) nor individual recognition of opponents (Gherardi and Tiedemann 2004a,b; Gherardi and Atema 2005b) have an effect, but winners (and losers) were always the crabs occupying larger (and smaller) shells, notwithstanding their experience of repeated losses (and wins).

However, the memory of shells of different quality may lead to a significant intensification of aggression (more numerous fights, higher average score, more frequent strong contacts and attacks by the new subordinate crab, independent of the defender, in Expt. 5 than in Expt. 2). This was not due to the possible disturbance inflicted on the crabs through their manipulation (it was in fact shown also by β , which was not subject to any manipulation). Crabs (specifically α and γ) seemed to perceive a change from their recent past in the subjective value of the held resource and drastically modified their behavior, the old α , now behaving as γ , and the old γ , now behaving as α . Future studies are needed to rigorously examine whether and how

crabs can assess the difference between past and present shells, and behave accordingly.

Acknowledgements The study was made possible by MBL Associates, Ann E. Kammer Memorial Fellowship Fund, H. Keffer Hartline Fellowship Fund, Frank R. Lillie Fund, and the Plum Foundation. The author thanks two anonymous referees for their valuable comments on the manuscript.

References

- Angel JE (2000) Effects of shell fit on the biology of the hermit crab *Pagurus longicarpus* (Say). *J Exp Mar Biol Ecol* 243:169–184
- Archer J (1988) The behavioural biology of aggression. Cambridge University Press, Cambridge
- Austad SN (1983) A game theoretical interpretation of male combat in the bowl and doily spider (*Frontinella pyramitela*). *Anim Behav* 31:59–73
- Barnard C, Brown C (1982) The effects of prior residence, competitive ability and food availability on the outcome of interactions between shrews. *Behav Ecol Sociobiol* 10:307–312
- Bertness MD (1980) Shell preference and utilization patterns in littoral hermit crabs of the Bay of Panama. *J Exp Mar Biol Ecol* 48:1–16
- Bertness MD (1981a) The influence of shell-type on hermit crab growth rate and clutch size (Decapoda, Anomura). *Crustaceana* 40:197–205
- Bertness MD (1981b) Predation, physical stress and the organization of a tropical rocky intertidal hermit crab community. *Ecology* 62:411–425
- Bertness MD (1981c) Conflicting advantages in resource utilization: the hermit crab housing dilemma. *Am Nat* 118:432–437
- Borjesson DL, Szelistowski WA (1989) Shell selection, utilization and predation in the hermit crab *Clibanarius panamensis* Stimpson in a tropical mangrove estuary. *J Exp Mar Biol Ecol* 133:213–228
- Briffa M, Elwood RW (2000a) Analysis of the finescale timing of repeated signals: does shell rapping in hermit crabs signal stamina? *Anim Behav* 59:159–165
- Briffa M, Elwood RW (2000b) The power of shell rapping influences rates of eviction in hermit crabs. *Behav Ecol* 11:288–293
- Briffa M, Elwood RW (2001) Decision rules, energy metabolism and vigor of hermit crab fights. *Proc R Soc Lond B* 268:1841–1848
- Briffa M, Elwood RW (2002) Power of shell-rapping signals influences physiological costs and subsequent decisions during hermit crab fights. *Proc R Soc Lond B* 269:2331–2336
- Briffa M, Elwood RW (2004) Use of energy reserves in fighting hermit crabs. *Proc R Soc Lond B* 271:373–379
- Burmeister S, Ophir AG, Ryan MJ, Wilczynski W (2002) Information transfer during cricket frog contests. *Anim Behav* 64:715–725
- Caldwell RL, Dingle J (1979) The influence of size differential on agonistic encounters in the mantis shrimp, *Gonodactylus viridis*. *Behaviour* 69:257–264
- Chase ID (1982) Dynamics of hierarchy formation: the sequential development of dominance relationships. *Behaviour* 80:218–240
- Chase ID, Tovey C, Spangler-Martin D, Manfredonia M (2002) Individual differences versus social dynamics in the formation of animal dominance hierarchies. *Proc Natl Acad Sci U S A* 99:5744–5749
- Childress JR (1972) Behavioral ecology and fitness theory in a tropical hermit crab. *Ecology* 53:960–964
- Clutton-Brock TH, Albon SD, Gibson RM, Guinness FE (1979) The logical stag: adaptive aspects of fighting in red deer (*Cervus elaphus* L.). *Anim Behav* 27:211–225

- Côté IM, Reverdý B, Cooke PK (1998) Less choosy or different preference? Impact of hypoxia on hermit crab shell assessment and selection. *Anim Behav* 56:867–873
- Davenport J, Busschots PM, Cawthorne DF (1980) The influence of salinity on behaviour and oxygen uptake of the hermit crab *Pagurus bernhardus* L. *J Mar Biol Assoc UK* 60:127–134
- Davies NB (1978) Territorial defence in the speckled wood butterfly (*Pararge aegeria*): the resident always wins. *Anim Behav* 26:138–147
- Daws AG, Grills J, Konzen K, Moore PA (2002) Previous experiences alter the outcome of aggressive interactions between males in the crayfish, *Procambarus clarkii*. *Mar Fresh Behav Physiol* 35:139–148
- Dearborn DC (1998) Interspecific territoriality by a rufous-tailed hummingbird (*Amazilia tzacatl*): effects of intruder size and resource value. *Biotropica* 30:306–313
- Dowds BM, Elwood RW (1985) Shell wars 2: the influence of relative size on decisions made during hermit crab shell fights. *Anim Behav* 33:649–656
- Drews C (1993) The concept and definition of dominance in animal behaviour. *Behaviour* 125:283–313
- Dugatkin LA (1997) Winner and loser effects and structure of dominance hierarchies. *Behav Ecol* 8:583–587
- Elwood RW (1995) Motivational changes during resource assessment by hermit crabs. *J Exp Mar Biol Ecol* 193:41–55
- Elwood RW, Glass CW (1981) Negotiation or aggression during shell fights of the hermit crab, *Pagurus bernhardus*. *Anim Behav* 29:1239–1244
- Elwood RW, Neil SJ (1992) Assessment and decisions: a study of information gathering by hermit crabs. Chapman and Hall, London
- Elwood RW, Marks N, Dick JTA (1995) Consequences of shell-species preferences for female reproductive success in the hermit crab *Pagurus bernhardus*. *Mar Biol* 123:431–434
- Elwood RW, Wood KE, Gallagher MB, Dick JTA (1998) Probing motivational state during agonistic encounters in animals. *Nature* 393:66–68
- Enquist M, Leimar O (1983) Evolution of fighting behaviour: decision rules and the assessment of relative strength. *J Theor Biol* 102:387–410
- Enquist M, Leimar O (1987) Evolution of fighting behaviour: the effect of variation in resource value. *J Theor Biol* 127:187–205
- Ewald P (1985) Influences of asymmetries in resource quality and age on aggression and dominance in black-chinned hummingbirds. *Anim Behav* 33:705–719
- Fotheringham N (1976a) Effects of shell stress on the growth of hermit crabs. *J Exp Mar Biol Ecol* 23:299–305
- Fotheringham N (1976b) Population consequences of shell utilization by hermit crabs. *Ecology* 57:570–578
- Fotheringham N (1976c) Hermit crab shells as a limiting resource. *Crustaceana* 31:194–197
- Fotheringham N (1980) Effects of shell utilization on reproductive patterns of tropical hermit crabs. *Mar Biol* 55:287–293
- Gherardi F (1996a) Non-conventional hermit crabs: pros and cons of sessile, tube-dwelling life in *Discorsopagurus schmitti* (Stevens). *J Exp Mar Biol Ecol* 202:119–136
- Gherardi F (1996b) Effects of shell status and social context on the agonistic behavior of the tropical hermit crab, *Clibanarius signatus*. *J Ethol* 14:111–121
- Gherardi F, Atema J (2005a) Effects of chemical context on shell investigation behavior in hermit crabs. *J Exp Mar Biol Ecol* 320:1–7
- Gherardi F, Atema J (2005b) Memory of social partners in hermit crab dominance. *Ethology* 111:271–285
- Gherardi F, Cioni A (2004) Agonism and interference competition in freshwater decapods. *Behaviour* 141:1297–1324
- Gherardi F, Daniels WH (2003) Dominance hierarchies and status recognition in the crayfish, *Procambarus acutus acutus*. *Can J Zool* 81:1269–1281
- Gherardi F, Tiedemann J (2004a) Binary individual recognition in hermit crabs. *Behav Ecol Sociobiol* 55:524–530
- Gherardi F, Tiedemann J (2004b) Chemical cues and binary individual recognition in the hermit crab, *Pagurus longicarpus*. *J Zool Lond* 263:23–29
- Gherardi F, Tricarico E, Atema J (in press) Unraveling the nature of individual recognition by odor in hermit crabs. *J Chem Ecol*
- Gherardi F, Zatterli F, Vannini M (1994) Hermit crabs in a mangrove swamp: the structure of *Clibanarius laevimanus* clustering. *Mar Biol* 121:41–52
- Gilley DC (2001) The behavior of honey bees (*Apis mellifera ligustica*) during queen duels. *Ethology* 107:601–622
- Grant WC, Ulmer KM (1974) Shell selection and aggressive behavior in two sympatric species of hermit crabs. *Biol Bull* 146:32–43
- Hazlett BA (1966a) Social behavior of the Paguridae and Diogenidae of Curaçao. *Stud Fauna Curaçao Other Caribb Isl* 23:1–143
- Hazlett BA (1966b) Factors affecting the aggressive behavior of the hermit crab *Calcinus tibicen*. *Z Tierpsychol* 23:655–671
- Hazlett BA (1970a) The effect of shell size and weight on the agonistic behavior of a hermit crab. *Z Tierpsychol* 27:369–374
- Hazlett BA (1970b) Tactile stimuli in the social behavior of *Pagurus bernhardus* (Decapoda, Paguridae). *Behaviour* 36:20–48
- Hazlett BA (1978) Shell exchanges in hermit crabs: aggression, negotiation or both? *Anim Behav* 26:1278–1279
- Hazlett BA (1980) Communication and mutual resource exchange in North Florida hermit crabs. *Behav Ecol Sociobiol* 6:177–184
- Hazlett BA (1981) The behavioral ecology of hermit crabs. *Annu Rev Ecol Syst* 12:1–22
- Hazlett BA (1987) Information transfer during shell exchange in the hermit crab *Clibanarius antillensis*. *Anim Behav* 35:218–226
- Hazlett BA (1989) Mating success of male hermit crabs in shell generalist and shell specialist species. *Behav Ecol Sociobiol* 25:119–128
- Hazlett BA (1996) Assessment during shell exchanges by the hermit crab *Clibanarius vittatus*: the complete negotiator. *Anim Behav* 51:567–573
- Herreid CF, Full RJ (1986) Energetics of hermit crabs during locomotion: the cost of carrying a shell. *J Exp Biol* 120:297–308
- Huntingford F, Turner A (1987) Animal conflict. Chapman and Hall, New York
- Jackson NW, Elwood RW (1989) Memory of information gained during shell investigation by the hermit crab, *Pagurus bernhardus*. *Anim Behav* 37:529–534
- Jennings DJ, Gammell MP, Carlin CM, Hayden TJ (2004) Effect of body weight, antler length, resource value and experience on fight duration and intensity in fallow deer. *Anim Behav* 68:213–221
- Karavanich C, Atema J (1998) Individual recognition and memory in lobster dominance. *Anim Behav* 56:1553–1560
- Katz J, Rittschof D (1993) Alarm/investigation responses of hermit crabs as related to shell fit and crab size. *Mar Behav Physiol* 22:171–182
- Kellogg CW (1976) Gastropod shells: a potential limiting resource for hermit crabs. *J Exp Mar Biol Ecol* 22:101–111
- Lindström K, Pampoulie C (2005) Effects of resource holding potential and resource value on tenure at nest sites in sand gobies. *Behav Ecol* 16:70–74
- López P, Martín J (2001) Fighting rules and rival recognition reduce costs of aggression in male lizards, *Podarcis hispanica*. *Behav Ecol Sociobiol* 49:111–116
- Markham JC (1968) Notes on growth-patterns and shell utilization of the hermit crab *Pagurus bernhardus*. *Ophelia* 5:189–205
- Maynard Smith J (1974) The theory of games and the evolution of animal conflicts. *J Theor Biol* 47:209–221
- Maynard Smith J (1982) Evolution and the theory of games. Cambridge University Press, Cambridge, UK
- Maynard Smith J, Parker GA (1976) The logic of asymmetric contests. *Anim Behav* 24:159–175
- Mesterton-Gibbons M, Marden JH, Dugatkin LA (1996) On wars of attrition without assessment. *J Theor Biol* 181:65–83

- Neil SJ, Elwood RE (1986) Factors influencing shell investigation in the hermit crab, *Pagurus bernhardus*. *Ethology* 73:225–234
- Parker GA (1974) Assessment strategy and the evolution of fighting behaviour. *J Theor Biol* 47:223–243
- Parker GA, Rubenstein DI (1981) Role assessment, reserve strategy, and acquisition of information in animal contests. *Anim Behav* 29:221–240
- Payne RJH (1998) Gradually escalating fights and displays: the cumulative assessment model. *Anim Behav* 56:651–662
- Payne RJH, Pagel M (1996) Escalation and time costs in displays of endurance. *J Theor Biol* 183:185–193
- Provenzano AJ Jr (1960) Notes on Bermuda hermit crabs (Crustacea; Anomura). *Bull Mar Sci* 10:117–124
- Rand WM, Rand AS (1976) Agonistic behaviour in nesting iguanas: a stochastic analysis of dispute settlement dominated by the minimization of energy cost. *Z Tierpsychol* 40:279–299
- Reese ES (1969) Behavioral adaptations of intertidal hermit crabs. *Am Zool* 9:343–355
- Rittschof D (1980a) Chemical attraction of hermit crabs and other attendants to gastropod predation sites. *J Chem Ecol* 6:103–118
- Rittschof D (1980b) Enzymatic production of small molecules attracting hermit crabs to simulated predation sites. *J Chem Ecol* 6:665–676
- Rittschof D, Sarrica J, Rubenstein D (1995) Shell dynamics and microhabitat selection by striped legged hermit crabs, *Clibanarius vittatus* (Bosc). *J Exp Mar Biol Ecol* 192:157–172
- Rutheford JD (1977) Removal of living snails from their shells by a hermit crab. *Veliger* 19:438–439
- Scully EP (1979) The effects of gastropod shell availability and habitat characteristics on shell utilization by the intertidal crab *Pagurus longicarpus* Say. *J Exp Mar Biol Ecol* 37:139–152
- Scully EP (1986) Shell investigation behavior of the intertidal hermit crab *Pagurus longicarpus* Say. *J Crust Biol* 6:749–756
- Siegel S, Castellan NJ Jr (1988) Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York
- Sneddon LU, Huntingford FA, Taylor AC (1997) Weapon size versus body size as a predictor of winning in fights between shore crabs, *Carcinus maenas* (L.). *Behav Ecol Sociobiol* 41:237–242
- Sneddon LU, Taylor AC, Huntingford FA (1999) Metabolic consequences of agonistic behaviour: crab fights in declining oxygen tensions. *Anim Behav* 57:353–363
- Sokal RR, Rohlf FJ (1969) Biometry. Freeman, San Francisco
- Taylor PR (1981) Hermit crab fitness: the effect of shell condition and behavioral adaptations on environmental resistance. *J Exp Mar Biol Ecol* 52:205–218
- Taylor PW, Elwood RW (2003) The mis-measure of animal contests. *Anim Behav* 65:1195–1202
- Taylor PW, Hasson O, Clark DL (2001) Initiation and resolution of jumping spider contests: roles for size, proximity, and early detection of rivals. *Behav Ecol Sociobiol* 50:403–413
- Thornhill R (1984) Fighting and assessment in *Harpobittacus* scorpionflies (Insecta: Mecoptera). *Evolution* 38:204–214
- Tobias J (1997) Asymmetric territorial contests in the European robin: the role of settlement costs. *Anim Behav* 54:9–21
- Vance RR (1972a) The role of shell adequacy in behavioral interactions involving hermit crabs. *Ecology* 53:1075–1083
- Vance RR (1972b) Competition and mechanism of coexistence in three sympatric species of intertidal hermit crabs. *Ecology* 53:1062–1074
- Vance RR (1973) The role of shell adequacy in behavioral interactions involving hermit crabs. *Ecology* 53:1075–1083
- Vye C, Cobb JS, Bradley T, Gabbay J, Genizi A, Karplus I (1997) Predicting the winning or losing of symmetrical contests in the American lobster *Homarus americanus* (Milne-Edwards). *J Exp Mar Biol Ecol* 217:19–29
- Wada S, Ohmori H, Goshima S, Nakao S (1997) Shell size preference of hermit crabs depends on their growth rate. *Anim Behav* 54:1–8
- Wilber TP (1989) Associations between gastropod shell characteristics and egg production in the hermit crab *Pagurus longicarpus*. *Oecologia* 81:6–15
- Wilber TP (1990) Influence of size, species and damage on shell selection by the hermit crab *Pagurus longicarpus*. *Mar Biol* 104:31–39
- Wilber TP, Herrnkind WF (1984) Predaceous gastropods regulate new-shell supply to salt marsh hermit crabs. *Mar Biol* 79:145–150
- Williams AB (1984) Shrimps, lobsters, and crabs of the Atlantic coast of the Eastern United States, Maine to Florida. Smithsonian Institution Press, Washington, DC
- Winston M, Jacobson S (1978) Dominance and effects of strange conspecifics on aggressive interactions in the hermit crab *Pagurus longicarpus*. *Anim Behav* 26:184–191
- Wittenberger JF (1981) Animal social behavior. Duxbury Press, Boston
- Ydenberg RC, Giraldeau LA, Falls JB (1988) Neighbors, strangers, and the asymmetric war of attrition. *Anim Behav* 36:343–347
- Zulandt RA, Schneider RWS, Moore PA (1999) Recognition of dominance status by chemoreception in the red swamp crayfish, *Procambarus clarkii*. *J Chem Ecol* 25:781–794